Changes in postprandial plasma and extracellular and ruminal fluid volumes in wethers fed or unfed for 72 hours[1,2,3]

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ABSTRACT: Postprandial shifts in body water compartments might limit feed intake by ruminants, especially when an animal becomes partially dehydrated during transportation or other periods of water deprivation. This experiment was conducted to determine the effects of feed and water deprivation on postprandial changes in body water compartments in wethers. Hampshire wethers (n = 8; average BW 42 ± 2 kg) were used in a crossover design. During each period, four wethers were limit-fed (540 g DM/d: FED) and four were deprived of feed and water for 72 h (DEPRIVED). Wethers were infused i.v. with Evans blue and sodium thiosulfate and intraruminally with Cr- or Co-EDTA, after which blood and ruminal samples were collected for the next 4 h. All wethers were then fed 540 g of feed DM, and infusions were repeated 30 min after feeding. Body water compartment volumes were determined with linear regression using plasma concentrations of Evans blue (plasma volume), and sodium thiosulfate (extracellular volume), and using ruminal fluid concentrations of Cr or Co. Feed and water deprivation decreased ($P < .01$) extracellular water space but did not affect plasma or ruminal water space. After feeding, extracelluar water space decreased ($P < .01$) and ruminal volume increased ($P < .05$) in the FED and DEPRIVED wethers. Plasma pools of Na, K, and Mg were not affected by feeding in FED wethers but decreased ($P < .05$) in DEPRIVED wethers. The increase in ruminal fluid pools of Na, K, and Mg were greater ($P < .05$) in FED than in DEPRIVED wethers. These results indicate that abnormal water and electrolyte shifts may be factors partially responsible for the decreased feed intake by ruminants subjected to transportation or feed and water deprivation stress.

Key Words: Body Water, Sheep, Deprivation, Stress

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Introduction

Carter and Grovum (1990a,b) suggested that ruminal osmotic shifts may affect short-term feed intake. Similarly, Ternouth (1968) and Christopherson and Webster (1972) hypothesized that tissue dehydration, caused by a shift of body water from the extracellular fluid to the ruminal contents during a meal, may be one factor responsible for satiety in ruminants fed highly digestible diets.

During periods of feed and water deprivation, such as those that occur during marketing and transportation of feeder cattle, appreciable losses of body weight and body water can occur (Cole et al., 1988a; Cole, 1995). Feeder calves stressed by marketing and transportation can have low feed intakes for 1 to 3 wk after arrival at a feedyard (Hutcheson and Cole, 1986). The cause(s) of the low feed intake are not yet known. Although some reports suggested that a decreased ruminal fermentative activity was involved (Cole and Hutcheson, 1985a,b), later reports suggested that depressed microbial activity was not critical (Cole, 1991; Fluharty et al., 1994, 1996) or that altered endocrine/metabolic patterns (Cole et al., 1988b, 1993; Cole, 1991) might also be involved.

In dehydrated ruminants, shifts in body water and electrolytes might be altered, resulting in decreased feed intake. Therefore, this study was conducted to determine the effects of feeding on plasma, extracellular, and ruminal volume in wethers that were continuously fed and in wethers that had been deprived of feed and water for 72 h to simulate a 24-h transportation period (Cole and Hutcheson, 1985b; Cole et al., 1988a).

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Materials and Methods

All surgical and experimental procedures were approved by the laboratory animal care committee, and animals were treated as prescribed (Consortium, 1988).

Mature Hampshire wethers (n = 8) averaging 42 ± 2 kg of BW and fitted with permanent ruminal cannulas were used in a crossover design. Each period of the crossover was 28 d. Wethers were housed indoors in individual pens (1.5 × 2.0 m) with slotted floors. Except during the 72-h feed and water deprivation period, wethers were limit-fed (540 g/d, DM basis) once daily a pelleted diet at 1300. The diet contained 52.6% cottonseed hulls, 18.6% corn, 14.1% cottonseed meal, 5% alfalfa, 5% molasses, and 4.7% vitamin and mineral supplement and was formulated to meet nutrient requirements (NRC, 1985). Ambient temperature within the facility was maintained at 17 to 20°C, and the relative humidity was maintained between 40 and 60%.

Starting on d 25 of each period of the crossover design, four wethers were deprived of feed and water for 72 h (**DEPRIVED**), and four wethers were fed the pelleted diet (**FED**) as during the adjustment phase. On d 2 of the deprivation period, all wethers were fitted with jugular catheters (Abbocath-T, 14 gauge × 14 cm, Abbott Hospitals, North Chicago, IL). At the end of the deprivation period, each wether was infused through the jugular catheter at 0800 with 5 mL of a .5% (wt/vol) Evans blue solution and 10 mL of a 10% (wt/vol) sodium thiosulfate solution, after which the catheter was flushed with a 3.5% (wt/vol) sodium citrate solution. At the same time, each wether was infused intraruminally with approximately 1 g of either Co- or Cr-EDTA (dissolved in 100 mL of water). Tubes containing the infusion solutions were weighed before and after the infusions to determine the actual quantity of solution infused. Water was not available to the wethers during the sampling period.

Blood samples were collected via the reciprocal jugular catheter in heparinized tubes at 0, 15, 30, 60, 120, 180, and 240 min after infusion and were immediately placed on ice. Blood was centrifuged at 3,000 × *g* for 30 min to recover plasma; however, a portion of the 0- and 240-min samples was frozen as whole blood. Plasma and whole blood samples were stored at −4°C.

Ruminal digesta samples were collected at 0, 1, 2, 3, and 4 h after infusions. The pH was measured immediately with a combination electrode, after which the samples were strained through six layers of cheesecloth and stored frozen.

Following the 240-min sample collection period, all wethers were allowed access to 540 g (DM basis) of the pelleted diet and had ad libitum access to water for 30 min. After feed and water were removed, wethers were again infused with the Evans blue, sodium thiosulfate, and either Co- or Cr-EDTA solutions as previously described. Wethers were infused with a different ruminal marker before and after feeding. Half the wethers were initially infused with Co-EDTA and half were initially infused with Cr-EDTA. Uden et al. (1980) and Teeter and Owens (1983) reported that Co-EDTA and Cr-EDTA give comparable results for ruminal volume measurements. Following the infusions, blood and ruminal samples were collected and processed as previously described.

Whole blood samples were analyzed immediately for packed cell volume (**PCV**) using microhematocrit centrifuge tubes. Whole blood, plasma, and ruminal fluid were analyzed for Na, K, and Mg using atomic absorption spectroscopy with an air + acetylene flame. Plasma samples were analyzed for glucose (Bittner and Manning, 1966), Evans blue (0, 15, 30, and 60 min samples; Hix, et al., 1959), and sodium thiosulfate (0, 30, 60, 120, 180, and 240 min samples; Ross, et al., 1992) using visible spectrophotometric procedures. Ruminal fluid samples were analyzed for Co or Cr using atomic absorption spectroscopy with an air + acetylene flame.

Plasma, extracellular, and ruminal fluid volumes were determined with log transformed regression analysis using the PROC REG procedures of SAS (1988). Evans blue was used to determine plasma volume, sodium thiosulfate was used to determine extracellular space, and Co or Cr were used to determine ruminal volume. During the postfeeding period, plasma concentrations of Evans blue and sodium thiosulfate were corrected for residual concentrations from the prefeeding period by extrapolating the curve from the prefeeding period to the time of dosing in the postfeeding period.

Data were analyzed statistically with ANOVA for a crossover design using the GLM procedures of SAS (1988). Time and treatment effects were analyzed as a split plot in time. The model contained effects for lamb, treatment (FED vs DEPRIVED), time (pre- or postfeeding), treatment × time interaction, and period. The lamb (treatment) mean square was used as the error term for treatment, and the residual mean square was used as the error term for time and the treatment × time interaction. If a significant treatment × time interaction was obtained, simple effects were compared with a F-test using ANOVA conducted within time and within treatment.

Results

During the 30-min feeding period, FED wethers consumed all the feed provided (540 g DM), whereas DEPRIVED wethers consumed an average of 438 ± 50 g DM ($P < .05$) of the pelleted diet (Table 1). As a result of lower feed intakes, DEPRIVED wethers had lower ($P < .05$) intakes of Na, K, and Mg than FED wethers (Table 1). Water consumption did not differ between FED and DEPRIVED wethers during the 30-min feeding period (Table 1).

Wethers that were FED had lower ($P < .01$) PCV than DEPRIVED wethers before (means 36 vs 43 ± .9%, respectively) and after (means 35 vs 42 ± 1.1%, respectively) feeding. Before feeding, FED wethers had greater ($P < .01$) plasma glucose concentrations than

Table 1. Feed and water intakes during the 30-min feeding period and plasma, extracellular, and ruminal volume of wethers fed each day (FED) or deprived of feed and water for 72 h before feeding (DEPRIVED) (n = 8)

Item	FED	DEPRIVED	SEM
Water intake, L	1.64	1.77	.66
Dry matter intake, g	540	438	50
Na intake, mg	1,890	1,379	157
K intake, mg	6,200	4,600	525
Mg intake, mg	1,188	867	99
Plasma, L[a]			
Prefeeding	1.95	1.84	.14
Postfeeding	1.93	1.56*	.08
Change	−.02	−.29	.13
Extracellular, L[a]			
Prefeeding	11.75	9.99**	.37
Postfeeding	10.82[b]	9.34**,[b]	.29
Change	−.93	−.64	.17
Ruminal, L			
Prefeeding	2.68	2.34	.16
Postfeeding	3.41[b]	3.42[b]	.48
Change	+.73	+1.08	.38
Ruminal dilution rate, %/h			
Prefeeding	8.04	8.64	.85
Postfeeding	15.06[b]	19.60[b]	2.03

[a]Time × treatment interaction ($P < .05$).
[b]Different from prefeeding ($P < .05$).
*Different from FED ($P < .05$).
**Different from FED ($P < .01$).

DEPRIVED wethers (62 vs 45 ± 1.4 mg/100 mL). Plasma glucose concentrations did not differ between FED and DEPRIVED wethers at 30 (64 vs 62 ± 1.8 mg/100 mL, respectively), 60 (71 vs 76 ± 2.0 mg/100 mL, respectively), and 120 (77 vs 78 ± 2.1 mg/100 mL, respectively) min postfeeding.

Ruminal fluid pH values (Figure 1) were greater ($P < .01$) in DEPRIVED than in FED wethers at each sampling time. After feeding, ruminal pH decreased ($P < .01$) from 6.9 to 5.6 in DEPRIVED wethers and from 6.2 to 5.0 in FED wethers.

Body Water Compartments. Plasma volumes (Table 1) were not different ($P > .10$) in FED and DEPRIVED wethers before feeding; however, after feeding, DEPRIVED wethers had lower ($P < .05$) plasma volume than FED wethers. In FED wethers, plasma volume did not change after feeding, whereas, in DEPRIVED wethers, plasma volume decreased 16% ($P < .05$) after feeding.

Extracellular water volume was greater ($P < .01$) in FED than in DEPRIVED wethers before and after feeding (Table 1). Extracellular water volumes decreased after feeding in both FED ($P < .01$) and DEPRIVED ($P < .05$) wethers; the decrease was numerically greater in FED than in DEPRIVED wethers.

Ruminal volumes did not differ between FED and DEPRIVED wethers before and after feeding (Table 1). After feeding, ruminal volumes increased ($P < .05$) in the FED and DEPRIVED wethers. Ruminal dilution rates were not affected by feed and water deprivation but were greater ($P < .05$) after feeding than before feeding in FED and DEPRIVED wethers.

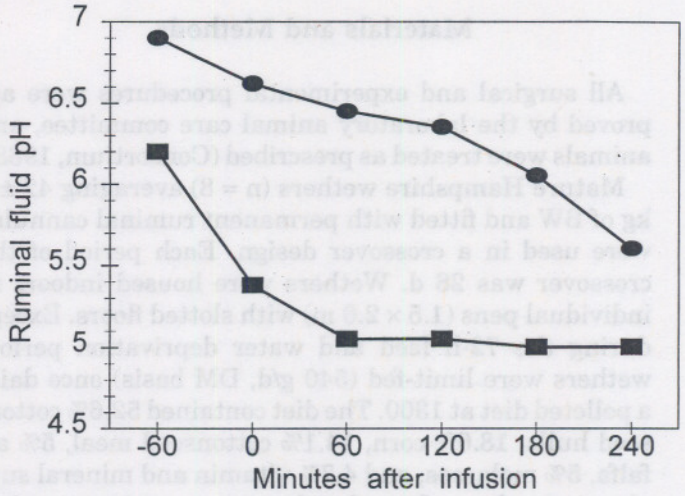

Figure 1. Postfeeding ruminal pH of wethers fed each day (FED) or deprived of feed and water for 72 h before feeding (DEPRIVED). Feed and water were provided to all wethers at –60 min and were removed at –30 min. At 0 min, wethers were infused i.v. with Evans blue and sodium thiosulfate and intraruminally with Co- or Cr-EDTA. Closed circles = DEPRIVED, Closed squares = FED. (n = 8)

Electrolyte Pools. Plasma Na and Mg concentrations were not affected by deprivation or feeding (Table 2). Plasma K concentrations were lower in DEPRIVED than in FED wethers both prefeeding ($P < .05$) and postfeeding ($P < .10$). Plasma K concentrations increased ($P < .05$) after feeding in FED wethers but were not affected ($P > .10$) in DEPRIVED wethers.

Table 2. Plasma sodium, potassium, and magnesium concentrations of wethers fed each day (FED) or deprived of feed and water for 72 h before feeding (DEPRIVED) (n = 8)

Item	FED	DEPRIVED	SEM
Sodium, mEq/L			
Prefeeding	133.6	136.7	1.20
Postfeeding, 30 min	132.5	133.0	1.56
Postfeeding, 240 min	134.7	136.5	1.30
Potassium, mEq/L[a]			
Prefeeding	5.75	5.29*	.12
Postfeeding, 30 min	5.92	5.38†	.18
Postfeeding, 240 min	6.15[b]	5.53†	.15
Magnesium, mEq/L[a]			
Prefeeding	.94	.87	.03
Postfeeding, 30 min	.96	.86	.03
Postfeeding, 240 min	.98	.88†	.03

[a]Time × treatment interaction ($P < .05$).
[b]Different from prefeeding ($P < .05$).
†Different from FED ($P < .10$).
*Different from FED ($P < .05$).

Table 3. Whole-blood sodium, potassium, and magnesium concentrations of wethers fed each day (FED) or deprived of feed and water for 72 h before feeding (DEPRIVED) (n = 8)

Item	FED	DEPRIVED	SEM
Sodium, mEq/L			
Prefeeding	114.7	114.2	1.66
Postfeeding, 30 min	120.3[a]	119.1[b]	1.36
Postfeeding, 240 min	121.9[a]	119.4[b]	1.39
Potassium, mEq/L			
Prefeeding	10.16	10.03	.61
Postfeeding, 30 min	10.00	10.09	.56
Postfeeding, 240 min	10.07	9.83	.54
Magnesium, mEq/L			
Prefeeding	1.09	1.02	.03
Postfeeding, 30 min	1.10	1.06	.02
Postfeeding, 240 min	1.08	1.03	.03

[a]Different from prefeeding ($P < .05$).
[b]Different from prefeeding ($P < .10$).

Whole-blood Na, K, and Mg concentrations did not differ between FED and DEPRIVED wethers at the end of the deprivation period (Table 3). Whole-blood Na concentrations increased after feeding in the FED ($P < .05$) and DEPRIVED ($P < .10$) wethers, whereas whole-blood K and Mg concentrations were not affected by feeding.

At the end of the deprivation period, ruminal fluid concentrations of Na were lower ($P < .01$) in FED than in DEPRIVED wethers (Table 4). Feeding did not affect ($P > .10$) ruminal fluid Na concentrations in FED wethers but decreased ($P < .01$) Na concentrations in DEPRIVED wethers. Ruminal fluid Na concentrations were not different ($P > .10$) between FED and DEPRIVED wethers after eating.

Table 4. Ruminal fluid sodium, potassium, and magnesium concentrations of wethers fed each day (FED) or deprived of feed and water for 72 h before feeding (DEPRIVED) (n = 8)

Item	FED	DEPRIVED	SEM
Sodium, mEq/L[a]			
Prefeeding	98.8	124.8**	7.09
Postfeeding, 30 min	107.2	81.4[b]	8.15
Postfeeding, 240 min	102.5	99.0[b]	6.11
Potassium, mEq/L[a]			
Prefeeding	42.29	37.10	4.46
Postfeeding, 30 min	82.85[b]	38.72*	8.24
Postfeeding, 240 min	70.93[b]	47.33[†,c]	5.30
Magnesium, mEq/L[a]			
Prefeeding	3.03	.78**	.54
Postfeeding, 30 min	14.08[b]	1.53**[,c]	2.07
Postfeeding, 240 min	12.05[b]	5.77[†,b]	1.54

[a]Time × treatment interaction ($P < .01$).
[b]Different from prefeeding ($P < .01$).
[c]Different from prefeeding ($P < .10$).
[†]Different from FED ($P < .10$).
*Different from FED ($P < .05$).
**Different from FED ($P < .01$).

Table 5. Plasma and ruminal fluid Na, K, and Mg pools before and after feeding in wethers fed each day (FED) or deprived of feed and water for 72 h before feeding (DEPRIVED) (n = 8)

Item	FED	DEPRIVED	SEM
Plasma Na, mg[a]			
Prefeeding	5,922	5,711	397
Postfeeding	5,889	4,763*[,b]	243
Change	−32	−948	395
Plasma K, mg[a]			
Prefeeding	478	421	38
Postfeeding	444	329*[,c]	21
Change	−34	−92	36
Plasma Mg, mg[a]			
Prefeeding	44	38	3.2
Postfeeding	46	32**	2.7
Change	2	−6	2.9
Ruminal fluid Na, mg[a]			
Prefeeding	5,304	6,612[†]	465
Postfeeding	8,357[c]	6,528[†]	1,256
Change	3,052	−84*	1,095
Ruminal fluid K, mg[a]			
Prefeeding	5,071	3,896	526
Postfeeding	10,261[d]	5,720**[,c]	1,528
Change	5,190	1,823*	1,506
Ruminal fluid Mg, mg[a]			
Prefeeding	279	49**	34
Postfeeding	1,059[d]	151**[,c]	160
Change	780	102**	135

[a]Time × treatment interaction ($P < .05$).
[b]Different from prefeeding ($P < .09$).
[c]Different from prefeeding ($P < .05$).
[d]Different from prefeeding ($P < .01$).
[†]Different from FED ($P < .10$).
*Different from FED ($P < .05$).
**Different from FED ($P < .01$).

Concentrations of K in ruminal fluid before feeding did not differ between FED and DEPRIVED wethers (Table 4). Ruminal fluid K concentrations increased ($P < .01$) postfeeding in FED wethers. In DEPRIVED wethers, ruminal fluid K concentrations were similar to prefeeding values at 30 min postfeeding but tended ($P < .10$) to be higher at 240 min postfeeding. The FED wethers had greater concentrations of K in ruminal fluid than DEPRIVED wethers at 30 ($P < .05$) and 240 ($P < .10$) min after feeding.

At the end of the deprivation period, Mg concentrations in ruminal fluid were greater ($P < .01$) in FED than in DEPRIVED wethers (Table 4). Ruminal fluid Mg concentrations increased ($P < .01$) in the FED and DEPRIVED wethers after feeding. Fed wethers had higher ($P < .01$) ruminal fluid Mg concentrations than DEPRIVED wethers at 30 ($P < .01$) and 240 ($P < .10$) min after feeding.

Before feeding, plasma Na, K, and Mg pool sizes did not differ between FED and DEPRIVED wethers (Table 5). However, after feeding, FED wethers had larger plasma Na ($P < .05$), K ($P < .05$) and Mg ($P < .01$) pool sizes than DEPRIVED wethers. This was due to a decrease in the plasma Na ($P < .09$) and K ($P < .05$)

pool sizes and a numerical decrease in the plasma Mg pool size of DEPRIVED wethers during the 30-min feeding period. In contrast, the total plasma Na, K, and Mg pool sizes of FED wethers were not affected by feeding.

Before feeding, FED wethers tended ($P < .10$) to have smaller ruminal fluid Na and had greater ($P < .01$) ruminal fluid Mg pool sizes than DEPRIVED wethers (Table 5). After feeding, FED wethers had greater ruminal fluid Na ($P < .10$), K ($P < .01$), and Mg ($P < .01$) pool sizes than DEPRIVED wethers. The quantities of Na ($P < .05$), K ($P < .01$), and Mg ($P < .01$) in ruminal fluid pools of FED wethers increased during the 30-min feeding period (Table 5). The quantity of Na in ruminal fluid of DEPRIVED wethers was not affected ($P > .10$) by feeding. The ruminal fluid K and Mg pool sizes of DEPRIVED wethers increased ($P < .05$) after feeding. However, the magnitude of the increase was greater ($P < .05$ for Na and K; $P < .01$ for Mg) in FED than in DEPRIVED wethers.

Discussion

The decreased feed intake of DEPRIVED wethers agrees with previous studies in which a decreased feed intake and a slower rate of feed consumption was observed in lambs deprived of feed and water for 3 d (Cole et al., 1988b; Cole, 1991). The effects of the 3-d feed and water deprivation period on PCV (Cole and Hutcheson, 1985a; Cole et al., 1988a), plasma glucose concentrations (Cole, et al., 1988b, 1993), and ruminal pH (Cole and Hutcheson, 1985a,b) also agreed with previous reports.

In contrast to the results of Christopherson and Webster (1972), PCV values obtained in the present study were not affected by feeding. This finding may have been the result of sampling times because Christopherson and Webster (1972) noted the increase in PCV that occurred during feeding was transitory, with values returning to normal 30 min after feeding.

Body Water Compartments. The effects of feed and water deprivation on plasma volume agree with a previous study (Cole, 1995) that reported plasma volume was not affected by a 72-h feed and water deprivation period in sheep. Blair-West and Brook (1969) and Christopherson and Webster (1972) noted a decrease in plasma volume of sheep during a meal and ascribed the decrease to postprandial movement of water from the plasma to the ruminal contents. In the present study, the plasma volume of FED wethers did not change during feeding, whereas the decrease in plasma volume of DEPRIVED wethers during feeding (150 to 300 mL) was similar to results of Blair-West and Brook (1969) and Christopherson and Webster (1972). As with PCV, Christopherson and Webster (1972) noted that the decrease in plasma volume was transient and that plasma volumes returned to normal within 30 min after the onset of eating. Thus, the lack of a postfeeding change in plasma volume of FED wethers in the present study may have been the result of the sampling time used (30 min after feeding). The 16% decrease in plasma volume of DEPRIVED wethers during feeding suggests that the postprandial repletion of plasma volume in DEPRIVED wethers was slower than in FED wethers. A slower repletion of plasma volume in DEPRIVED wethers could be the result of several factors, including lower feed intake, a slower eating rate (Cole et al., 1988b), and(or) hormonal factors. During feeding, Blair-West and Brook (1969) noted a release of renin into the circulation of sheep, that ate rapidly, that was followed by renal conservation of Na and water within 30 min after eating. Plasma renin concentrations did not change in sheep that ate slowly. In agreement with previous studies (Cole, et al., 1988b), in the present study DEPRIVED wethers ate at a slower rate than FED wethers. It is not known whether this slower eating pattern in ruminants deprived of feed and water is related to renin secretion or other metabolic factors that occur during a meal.

The effects of feed and water deprivation on extracellular volume in the present study agree with the results obtained with bulls by Gortel et al (1992) but tend to contradict an earlier study (Cole, 1995) in which the loss in body water that occurred during a 72-h feed and water deprivation period was attributed to losses from the intracellular pool. A number of factors could potentially explain the discrepancy between results of the present study and those of Cole (1995). Dehydration normally begins as a decrease in extracellular water volume followed by an increase in plasma osmolality and a subsequent decrease in intracellular water volume (Greenleaf and Fregly, 1982). Thus, differences in the severity of the stress imposed and(or) the time of sampling after the stress is imposed could cause variations in the reported effects of stressors on body water pools. In our earlier study, sheep were heavier (72 kg) and consumed more feed (1,400 g/d in two meals). Thus, although animals were deprived of feed and water for 3 d in both the present study and the study of Cole (1995), the actual severity of the stress may have differed. In addition, in the previous study (Cole, 1995), extracellular volume was determined using sodium thiocyanate rather than sodium thiosulfate. Sodium thiocyanate concentrates in saliva (Christopherson and Webster, 1972) and, thus, can enter the rumen rapidly, but sodium thiosulfate does not enter the rumen for at least 3 h after i.v. infusion (Ternouth, 1968). Sodium thiosulfate also seems to equilibrate with extracellular water more rapidly than does sodium thiocyanate (Ross, et al., 1992).

The decrease in extracellular water volume noted during feeding in the present study was similar in magnitude to values reported by Ternouth (1968) and Christopherson and Webster (1972) (7 to 10%; .8 to 1.5 L) in sheep soon after eating. Ternouth (1968) noted that extracelluar volume returned to normal approximately 3 h after feeding and suggested that the decrease in volume of extracelluar fluid during a meal was the result of the high rate of salivary secretion associated

with feeding and the transfer of plasma fluids across the ruminal wall due to an osmotic gradient present after feeding. Christopherson and Webster (1972) suggested that considerable quantities of water from extracellular pools crossed the gut wall and entered the rumen when the sheep were eating because the decrease in extracellular volume was greater than the expected salivary flow. However, other studies suggest that the major source of the increased ruminal volume is salivary flow and that minimal quantities of water enter the ruminal digesta via transport across the ruminal wall from the plasma during a meal (Scott, 1975).

The effects of feed and water deprivation on ruminal fluid volume agree with previous studies that indicated a 3-d feed and water deprivation period does not appreciably affect ruminal fluid volume of sheep (Cole, 1991, 1995). Postfeeding changes in ruminal dilution rate were similar to those reported by Peters et al. (1990). The postfeeding increases in ruminal volume were smaller in magnitude than changes noted by Ternouth (1967) but greater than changes noted by Peters, et al. (1990). This may have been the result of differences in water consumption. Ternouth (1967) allowed animals access to water throughout the day, whereas Peters et al. (1990) withheld water during the dosing/sampling period. In the present study, the postprandial increase in ruminal volume was equal to approximately 44% of water intake in FED wethers and 61% of water intake in DEPRIVED wethers. The relatively small increases in ruminal volume compared with the quantity of water consumed could be interpreted to suggest a rapid absorption of water from the gut. However, the decrease in extracellular volume and increases in ruminal dilution rates suggest this is not the case. It is more likely that a rapid movement of water from the rumen to the lower GI tract occurred. Garza and Owens (1989) suggested that 60 to 80% of consumed water "bypassed" the rumen to the lower gut in steers. A high "bypass" of consumed water could explain the small increases in ruminal volume in relation to the total quantities of water (plasma, salivary, and consumed) that may have entered the rumen during the 30-min feeding period.

Electrolyte Pools. The effects of feeding on plasma electrolytes varied somewhat from previous studies. In the present study, feeding had no effect on plasma Na concentrations but caused an increase in plasma K concentrations 4 h postfeeding. In contrast, when sheep were fed 350 g of alfalfa chaff, Ternouth (1968) reported that feeding caused an increase in plasma Na concentrations but did not affect plasma K concentrations. These contrasting results may have occurred owing to differences in the mineral composition and(or) fermentability of the diets fed because Carr and Titchen (1978) ascribed the postfeeding increases in serum osmolality to absorption of osmotically active particles (VFA and electrolytes) from the rumen and to increased secretions from digestive glands. In FED wethers, feeding did not affect the size of plasma pools of Na, K, or Mg. However, the size of the plasma Na, K, and Mg pools were decreased in DEPRIVED wethers during feeding. This suggests that, in FED wethers, feeding did not cause an appreciable drain on the nonruminal electrolyte pools, whereas, when wethers had been deprived of feed and water for 3 d, feeding caused a marked drain on these electrolyte pools.

In FED wethers, the postfeeding changes in electrolyte concentrations of ruminal fluid agree with the results of Ternouth (1967) who reported that ruminal fluid K concentrations increased, and ruminal Na concentrations were not affected by feeding. The effects were similar both when sheep had access to water and when no water was provided during the feeding period (Ternouth, 1967). In the present study, ruminal fluid concentrations of K and Mg also increased postfeeding in DEPRIVED wethers, but the magnitude of the increase was less than in FED wethers. In addition, ruminal Na concentrations decreased in DEPRIVED wethers. Osmolality of ruminal fluid normally increases during a meal (Ternouth, 1967; Carter and Grovum, 1990a,b). Attempts to measure ruminal fluid osmolality using freezing point depression were unsuccessful in the present study. However, the greater concentrations of Na, K, and Mg in the ruminal fluid of FED wethers, as well as the greater ruminal concentrations of VFA that would be expected in FED wethers (Cole and Hutcheson, 1985a,b; Cole, 1991) suggest that the postfeeding increase in ruminal fluid osmolality was greater in FED than in DEPRIVED wethers.

The greater size of the prefeeding ruminal Na pool in DEPRIVED wethers suggests that the rumen is a major reservoir for Na during periods of feed and water deprivation. Because postfeeding changes in ruminal volume were similar in FED and DEPRIVED wethers, changes in the size of the ruminal Na, K, and Mg pools were similar to changes in electrolyte concentrations. Although intakes of Na, K, and Mg during the 30-min feeding period were different in FED and DEPRIVED wethers, the differences in ruminal electrolyte concentrations and pool sizes between FED and DEPRIVED wethers do not seem to be the result of differences in mineral intakes. The size of the ruminal fluid Na pool of DEPRIVED wethers was not affected by feeding, whereas, in FED wethers, the postprandial increase in the ruminal fluid Na pool (3,053 mg) averaged 162% of Na intake. The postprandial increase in the ruminal fluid pools of K (83% of intake) and Mg (65% of intake) in FED wethers were also greater than in DEPRIVED wethers (40% for K and 12% for Mg). These differences in ruminal electrolyte pool sizes of FED and DEPRIVED wethers may have been partially the result of differences in ruminal pH. Gaebel et al. (1987) noted that a low ruminal pH (4.8), similar to that noted for FED wethers in the present study, decreased the net absorption of Na from the rumen and led to a net secretion of Mg into the rumen.

Factors that control and(or) modify feed intake in normal, nonstressed ruminants have been extensively reviewed (Forbes, 1986; Owens, et al., 1995). Most stud-

ies have concentrated on factors affecting short-term feed intake. These controlling factors have been routinely classified into chemostatic, hormonal, peptide, and gut distention factors. It is still not clear how these factors may be related to the low feed intakes of ruminants subjected to stressors such as market transport, feed deprivation, and(or) dehydration. Lofgreen (1988) suggested that feed intake-controlling factors were different in "nonstressed" and "stressed" calves. He based this hypothesis on two factors: 1) when allowed to choose from diets containing different levels of energy, "stressed" calves selected a diet that was higher in energy than "nonstressed" calves and 2) in contrast to "nonstressed" calves, "stressed" calves ate greater quantities of a high-energy diet than of a low-energy diet.

Three related factors that control intake of moderate- to low-energy diets are rate of digestion, ruminal distension, and rate of passage (Forbes, 1986). We noted that ruminal fermentative capacity measured using a short-term gas production procedure was decreased by transport and by feed and water deprivation (Cole and Hutcheson, 1985a,b). There was an apparent relationship between the fermentative capacity of ruminal fluid and feed intake of food-deprived calves (Cole and Hutcheson, 1985b). However, with calves deprived of feed and water for a shorter period of time, Fluharty et al. (1994, 1996) noted no apparent relationship between feed intake and fermentative capacity measured using 24- to 48-h in situ digestion. We also noted that exchanging 50% of the ruminal contents of fed and unfed (3 d) sheep did not affect feed intake (Cole, 1991). Thus, ruminal microbial activity or rate of digestion do not seem to be critical factors controlling feed intake in ruminants subjected to feed deprivation or transport stressors.

The wet weight of the reticulorumen of sheep decreases by approximately 16% during a 3-d feed and water deprivation period (Cole, 1995). However, it is not clear whether the decrease in gut and ruminal weight is reflected in a decreased gut capacity. Such a change could potentially affect gut distention and(or) the rate of passage through the gut, thereby affecting diet digestion and(or) feed intake.

The plasma concentrations of many metabolites and hormones have been suggested as factors that influence or control feed intake in ruminants, with the most likely candidates being propionate, insulin, and glucagon (Forbes, 1986) The liver of ruminants is sensitive to glucose and propionate, especially when glycogen has been depleted by a period of feed deprivation (Forbes, 1986). Although a direct causal relationship was not established, we noted that feed intake, feeding pattern, and postprandial metabolite, insulin, and growth hormone changes differed in FED and DEPRIVED sheep (Cole et al., 1988b).

Carter and Grovum (1990a) suggested that the influx of water into the rumen during feeding could increase dilution rate and nutrient flow to the duodenum. Peters et al. (1990) noted a marked increase in ruminal dilution rate during the first 3 h postfeeding. Similar increases were noted in the present study. However, the increase in ruminal dilution rate was similar in both FED and DEPRIVED wethers, suggesting that it was not a factor controlling feed intake under the conditions of this experiment.

It has been suggested that the increases in ruminal fluid osmolality (Carter and Grovum, 1990a,b) and postprandial changes in extracellular volume and osmolality (Ternouth, 1968) may be factors controlling short-term feed intake in ruminants. Results of the present study confirm earlier reports indicating that appreciable movements of plasma, extracellular, and ruminal water and electrolytes occur in ruminants during a meal. The quantity and(or) timing of these water and electrolyte shifts seem to differ between animals that have been fed and animals that have been deprived of feed and water for several days.

Results of the present study do not establish a clear cause and effect relationship between water/electrolyte shifts and decreased feed intake in ruminants deprived of feed and water, but they may partially explain the decrease in carcass shrink (Schaefer, et al., 1990, 1992) and improvements in electrolyte balance (Cole, 1996) noted in transportation-stressed and feed-deprived ruminants when provided an electrolyte solution rather than water. Providing electrolyte solutions could potentially decrease salivary flow (Tomas and Potter, 1975) and renin secretion (Blair-West and Brook, 1969; Dahlborn, 1987), thereby decreasing the osmotic drain on body tissues that occurs during feeding, especially in partially dehydrated animals. The mechanisms governing the movement of ions and water across the ruminal epithelium seem to operate to minimize insults to the osmotic balance between plasma, interstitial fluid, cellular, and ruminal fluid of the animal. In partially dehydrated animals, this may require the animal to limit its feed intake to minimize adverse effects on osmotic balance.

Implications

Water and electrolyte shifts that normally occur in ruminants seem to differ between fed and unfed animals. These differences may be important in order to prevent or minimize insults to the osmotic balance of the animal when it is partially dehydrated. Altered ruminal fermentation, hormonal changes, and gut capacity have been implicated as possible causes of low feed intakes in calves and sheep subjected to marketing and transportation stress. If these osmotic shifts are important in controlling feed intake, nutritional and management techniques that could be developed to help counteract these shifts could potentially increase feed intake by cattle and sheep that have undergone transportation or other stressors.

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